
Guidelines for Subspecific Substitutions in Wildlife Restoration Projects

PHILIP J. SEDDON* AND PRITPAL S. SOORAE†

*National Wildlife Research Center, National Commission for Wildlife Conservation and Development, P.O. Box 1086, Taif, Kingdom of Saudi Arabia, email nwrc@compuserve.com

†IUCN/SSC Reintroduction Specialist Group, African Wildlife Foundation, P.O. Box 48177, Nairobi, Kenya, email psoorae@awfke.org

Abstract: *Reintroduction of animals is becoming increasingly popular as a means of restoring populations of threatened species. Sometimes depletion of wild populations leaves only captive populations from which reintroduction projects can obtain founders for releases. The World Conservation Union guidelines on reintroductions recommend that the individuals to be reintroduced should be of the same subspecies as those that were extirpated. In some cases, however, a subspecies may have become extinct in the wild and in captivity. A substitute form may then be chosen for possible release. Such substitutions are actually a form of benign introduction. Considerations include assessment of the value of a substitution project and the selection of a suitable substitute. Species substitutions increase biodiversity, conserve related forms, improve public awareness of conservation issues, educate the public, and may be implemented for aesthetic or economic reasons. Selection of a suitable substitute should focus on extant subspecies and consider genetic relatedness, phenotype, ecological compatibility, and conservation value of potential candidates. An example of a substitution project is the reintroduction of the North African Red-necked Ostrich (*Struthio camelus camelus*) into areas once occupied by the now extinct Arabian Ostrich (*Struthio camelus syriacus*). *S. c. camelus* was chosen as a substitute because of its geographic proximity, phenotypic similarity, and conservation value. The World Conservation Union's reintroduction guidelines should be consulted before a project is begun.*

Bases para la Substitución Subespecífica en Proyectos de Restauración de Vida Silvestre

Resumen: *La reintroducción de animales se ha vuelto muy popular como una medida para restaurar poblaciones de especies en peligro. Algunas veces la disminución de poblaciones silvestres deja únicamente poblaciones cautivas a partir de las cuales los proyectos de reintroducción pueden obtener los fundadores para sus liberaciones. Las bases de la Unión para la Conservación Mundial en materia de reintroducciones recomienda que los individuos a ser reintroducidos deben ser de la misma subespecie que aquellos que fueron extirpados. Sin embargo, en algunos casos, una subespecie puede haberse extinguido tanto en su hábitat como en cautiverio. Una forma substituta puede ser escogida para una posible liberación. Substituciones de este tipo son de hecho una forma benigna de introducción. Las consideraciones incluyen la evaluación de el valor de un proyecto de substitución y la selección de un substituto apto. La substitución de especies incrementa la biodiversidad, conserva las formas relacionadas, mejora la conciencia del público en asuntos de conservación, educa al público y puede ser implementada por razones estéticas o económicas. La selección de un substituto apto debe enfocarse en subespecies existentes y considerar la relación genética, fenotipo, compatibilidad económica y valor de conservación de los candidatos potenciales. Un ejemplo de un proyecto de substitución es la reintroducción del avestrúz de cuello rojo del norte de Africa (*Struthio camelus camelus*) en áreas que alguna vez fueron ocupadas por la extinta avestrúz árabe (*Struthio camelus syriacus*). *S. c. camelus* fue escogida como substituto debido a su proximidad geográfica, similitud en fenotipo y valor de conservación. Las bases para reintroducción de especies de la Unión para la Conservación Mundial deberían ser consultadas antes del inicio de los proyectos.*

Paper submitted October 13, 1997; revised manuscript accepted May 8, 1998.

Introduction

Restoration of a species to a region from which it has been extirpated may often be possible only through the release of new individuals. Where the species has become extinct in the wild or when suitable stock for reintroductions cannot be found from other areas, captive breeding and the release of captive-bred animals may be necessary. There has been a significant increase in the number of reintroduction projects worldwide. The Reintroduction Specialist Group (RSG) of the World Conservation Union (IUCN) estimates that between 1993 and 1997 there has been a 300% increase in the number of official reintroduction projects (World Conservation Union, unpublished data).

To have a chance of success, a reintroduction project, whether a wild-to-wild translocation or a release of captive-bred animals, needs careful planning and long-term commitment of resources. The IUCN's RSG has formulated reintroduction guidelines (IUCN 1995) that are now widely used in the planning, execution, and follow-up of reintroduction projects throughout the world.

Reduction or fragmentation of the population and range of a species may result in local or regional extinction, or even the extinction of the species in the wild (Gilpin & Soulé 1986; Gilpin 1987; Goodman 1987). Sometimes a species may become so threatened in the wild that it is taken into captivity, and the loss of wild animals may leave only captive populations. Examples include the Arabian oryx (*Oryx leucoryx*, Stanley Price 1989), Przewalski's horse (*Equus przewalskii*, Ryder 1988), the Socorro Dove (*Zenaidura macroura*, Walter 1993), and the Essex emerald moth (*Thetidia smaragdaria*, Hughes 1994). In such cases there is the potential to breed species in captivity, although the results of genetic and phenotypic changes such as genetic drift, inbreeding, domestication, increased tameness, and the loss of behavioral traits will tend to preclude the long-term preservation of a species through captive breeding (Snyder et al. 1996). Alternatively, attempts may be made to restore critically threatened species through the reintroduction of captive-bred animals into suitable habitat. Recent examples include programs for the black-footed ferret (*Mustela nigripes*, Clark 1994), the golden lion tamarin (*Leontopithecus rosalia*, Kleiman et al. 1988), and the red wolf (*Canis rufus*, Moore & Smith

1988). But if a subspecies has become extinct and thus no longer exists in the wild or in captivity there are two options: do nothing or attempt to fill the niche with a near relative.

The IUCN *Guidelines for Re-introductions* state that "... individuals to be re-introduced ... should preferably be of the same subspecies or race as those which were extirpated, unless adequate numbers are not available" (IUCN 1995:2). We consider this point and the case when the original subspecies has become extinct. We propose guidelines for the selection of the most appropriate extant form to replace an extinct subspecies, and we illustrate these with discussion of a current wildlife restoration project in Saudi Arabia, which uses a subspecific substitute to replace the extinct Arabian Ostrich (*Struthio camelus syriacus*).

Table 1 gives IUCN definitions for the types of reintroduction projects. We define a substitution project as a benign introduction of a subspecies or race considered the most suitable extant form to fill the ecological niche left vacant by the extinction of the original subspecies. The IUCN guidelines refer to species as the taxonomic unit but note that a lower taxonomic unit can be used (e.g., subspecies or race, as long as it can be unambiguously defined). We assume that definition of subspecies is possible and use subspecies as the taxonomic unit.

Substitution Project Considerations

Three questions need to be addressed before a substitution project is implemented: is there a need for it; what should be the substitute form; and is the project feasible?

Assessment of Need

Before a substitution project is initiated, consideration of one or more of the following factors may help determine whether such an undertaking is worthwhile: biodiversity and ecosystem stability, conservation of related forms, public awareness and education, and aesthetic and economic considerations.

The IUCN interprets biodiversity to encompass all species and ecosystem processes (Possiel et al. 1995). Biodi-

Table 1. Reintroduction guideline definitions (after IUCN 1995).

Term	Definition
Reintroduction	an attempt to establish a subspecies in an area that was once a part of its historical range, but from which it has been extirpated or become extinct
Translocation	deliberate and mediated movement of wild individuals or populations from one part of their range to another
Reinforcement/supplementation	addition of individuals to an existing population of conspecifics
Conservation/benign introduction	an attempt to establish a subspecies, for the purpose of conservation, outside its recorded distribution but within an appropriate habitat or ecogeographical area

versity may therefore be viewed at several levels, from genes to individuals and from populations, species, communities, and ecosystems to landscapes (Risser 1995). Ecosystem stability will depend on the maintenance of ecosystem processes and thus on each functional group of organisms. Where such groups have several equivalent species with differing sets of responses to disturbance, there is redundancy and ecosystem resilience. But if functional groups have only one or few species, then their functions within the ecosystem are lost with species extinction, and ecosystem stability will decrease (Walker 1995). Replacement of missing members of a functional group may increase ecosystem resilience in responding to disturbance.

Related forms may also be endangered in their normal range, and it may be possible to restore their numbers through introductions into habitat once occupied by an extinct form. Following the extinction of the British subspecies of the large copper butterfly (*Lycaena dispar dispar*), the Dutch subspecies (*Lycaena dispar batavus*) was selected for substitution due to its endangered status (Pullin 1993). The selection of related endangered forms will be important for the establishment of new populations or where a potential substitute is threatened by loss of natural habitat.

The release of high-profile "flagship" species may raise public awareness of conservation issues and generate funding for wider programs. In Saudi Arabia the first wildlife conservation project targeted the Houbara Bustard (*Chlamydotis [undulata] macqueenii*), which is threatened as a resident. Programs directed toward the Houbara have attracted wide public attention owing to the status of the bird in the Middle East as the premier quarry for Arab falconry (Seddon et al. 1995), and they will help generate support for other, lower-profile species in need of protection. A substitute form could similarly be used to focus public attention on conservation issues.

Protection of an area may be facilitated if this is for the benefit of a flagship species. Reserves totaling over 16,000 km² have been created in Saudi Arabia: two for the reintroduction of Arabian oryx and one for the protection of a remnant breeding population of Houbara Bustard. The protection of such large areas in Saudi Arabia is possible only with support generated through the focus on oryx and Houbara, yet the reserves are now refugia for an array of species for which direct conservation action would find little public sympathy.

The aesthetic value or economic benefits of an animal may also be tied to the generation of public support and the means to raise public awareness of conservation issues. From 1988 to 1990, lynx (*Felis lynx*) were released in New York state (U.S.A.). Public support is vital for carnivore reintroduction projects to succeed because carnivores may be dangerous both to livestock and occasionally to people. To secure goodwill and funding for this release, a public awareness program was built around the existing

appeal of felids (Brocke & Gustafson 1992). In Latvia the reintroduction of the beaver (*Castor fiber*) resulted in the creation and conservation of wetlands; their value in water purification has been estimated at up to 1.3 billion pounds sterling, and beavers reintroduced into France and Sweden have become tourist attractions (Macdonald et al. 1995).

Selection of a Substitute

The concept of species as a basic taxon unit is controversial. Attempts to define species have grouped organisms that share a common evolutionary fate, that are reproductively isolated, that share a common fertilization system, or that have the potential for genetic exchangeability through intrinsic cohesion mechanisms (Templeton 1989). An alternative idea is that there is no basic unit of taxa or evolution (Nelson 1989). Whatever the criteria used to assign an extinct form to a taxonomic category, we assumed that a substitute will be chosen from relatives that have been assigned according to the same criteria. In general, therefore, a substitute would be sought from among the extant subspecies or races because, by any of the mechanisms used to define species and speciation, substitute forms at or above the species level may be expected to have different habitat requirements. At the subspecies level, fewer fundamental differences in habitat preference may exist, and an introduction may function more as a range extension.

Considerations in listing potential substitutes are identification of the extant subspecies and ranking of candidates according to their genetic relatedness, phenotype, ecological compatibility, and conservation value. Molecular markers are now widely used to estimate the genetic relatedness of taxonomic units. Due to maternal and haploid inheritance without recombination and a relatively rapid pace of evolution, mitochondrial DNA analysis is preferred for systematic genetic studies at the intraspecific level (Avice 1995; but see Rand 1996). Although genetic analyses may be the best first stage in the selection of substitutes, testing may not be feasible due to funding constraints or may be impossible due to unavailability of tissue samples. Nevertheless, where possible, genetic study techniques should be applied to determine the relative relatedness between possible substitutes. Genetic analyses may also permit prediction of the likelihood of hybridization with other forms in the release region. In the southwestern United States, plans were made to capture a remnant population of red wolves to initiate a captive-breeding program. Out of 400 wild-caught canids, only 18 were genetically pure-bred wolves (Stanley Price et al. 1998).

Physical characteristics may be used as a guide to relatedness secondarily to genetic studies or when such studies are not possible. Although insensitive for fine-scale comparisons, use of museum specimens and old photographs may permit selection between potential candidates

on the basis of key physical features, particularly those of relevance to the substitute's ecological compatibility.

To have any chance of establishing a new population, the substitute form must be able to survive and thrive in the new site. As far as is possible it is necessary to compare information on the habitat and ecology of the extinct form with that of potential substitutes, including such factors as climate, geography, diet, breeding season, physical features of habitat, predators, and habitat use. A local population of ibex (*Capra ibex*) that became extinct in Czechoslovakia was replaced by reintroductions of Austrian *Capra ibex*, Turkish *Capra bircus aegagrus*, and *Capra ibex nubiana* from Sinai (reviewed in Stanley Price 1989). The inevitable hybrid forms dropped their kids in the middle of winter, three months earlier than pure *Capra ibex*, resulting in the death of all offspring; this case illustrates the need to assess both hybridization risks and ecological compatibility.

Assuming equal suitability and equal availability of two or more potential substitutes, final selection should take into consideration the conservation value of an introduction project for one form over others. Selection should favor the substitute that is most threatened, particularly when this threat comes from low numbers, fragmented populations, and restricted or reduced habitat.

Feasibility

Even given support for the value of a substitution and the selection of a suitable substitute form, the feasibility of the project must be assessed before funds are committed. Assessment of feasibility should consider the availability of habitat and animals, the reasons for the original extinction, the need for regional coordination and national controls, and the application of reintroduction guidelines.

In a review of the factors affecting success in wildlife translocations Wolf et al. (1996) found that, in addition to species suitability, success depended on the availability of sufficient suitable habitat. Assessment of habitat suitability should include the former distribution of the extinct form, the biology of potential substitutes, and the current status of habitat within the original distribution of the extinct form. Examination of the history, taxonomy, and biology of the target species and its close relatives was used to locate suitable habitat for the release of Przewalski's horse (van Dierendonck & Wallis de Vries 1996).

The second consideration Wolf et al. (1996) found important was the number of animals released. Examples of reintroduction projects in which the release of too few animals may have contributed to the projects' failure include those for Panamanian black-handed spider monkeys (*Ateles geoffroyi*), beavers in the Vistula River, and a pilot release of golden lion tamarins (review in Stanley Price 1989). The likelihood of successful establishment of introduced bird species in New Zealand was influenced by the number of individuals released (Green 1997). A primary

consideration is therefore whether sufficient animals can be secured without endangering the subspecies elsewhere. There may be political and financial constraints involved in obtaining sufficient numbers for release. One consideration is whether captive breeding is necessary and whether a captive-breeding facility exists or must be created. There has been a move for captive-breeding organizations to maximize their contribution to conservation (The World Zoo Organization [IUDZG] 1993; Balmford et al. 1996), and responsive zoos are likely to be willing participants in soundly based conservation projects (e.g., the Andean Condor [*Vultur gryphus*]; Lieberman et al. 1993).

It is essential that the causes of the original extinction be removed before any releases of a substitute take place. It is also important to determine whether there are other dangers the substitute could face. For example, the extinction of the original form may have been prompted by overhunting, but new threats posed by other human activities such as agriculture (Black bears [*Ursus americanus*]; Clark 1996) or poisoning and power lines (California Condor [*Gymnogyps californicus*]; Wallace 1992) may threaten a substitute.

Some form of regional coordination may be essential to ensure that the proposed project is compatible with other programs in the region. A primary consideration is whether the same substitute taxon is being used in neighboring substitutions. For migratory or dispersive species, securing suitable habitat may require cross-border agreements. International coordination may increase the efficiency of efforts and lower costs, while avoiding possible future conflicts.

The relevant national legislation governing the import of nonnative species should be consulted. On one hand, legislation may hamper the import of the substitute for release; on the other hand, lax regulations may allow relatively unregulated import of a variety of forms and lead to the possibility of accidental releases and interbreeding with the chosen substitute. Research should also consider whether legislation exists to protect the substitute at the release site. For instance, is the substitute covered by the same laws as was the extinct form?

Once a substitute has been chosen, the normal procedures for undertaking a reintroduction will apply, and the IUCN reintroduction guidelines (IUCN 1998) should be consulted. These guidelines call attention to additional details of veterinary screening and health checks on imported stock; pre-release handling and training; socio-economic studies and legal requirements; planning, preparation, and release stages and techniques; funding and manpower commitments; and post-release activities.

Case Study

One example of a conservation project that replaced an extinct form with a subspecies is the substitution of

North African Red-necked Ostrich for the Arabian Ostrich. We discuss this case according to the a posteriori application of the guidelines presented above.

The Arabian Ostrich became extinct in the wild in 1939 (Jennings 1986). No living specimens of the subspecies survive in any collections. The British Museum (Natural History) has two stuffed specimens, a male and a female, probably from the Al Jouf district in the north of Saudi Arabia (Jennings 1986).

Assessment of the Need for a Substitution

Saudi Arabia's rapid economic expansion after the 1940s brought with it increases in livestock and the opening of lands to free grazing. Combined with wood fuel gathering and cultivation, these two factors have reduced natural vegetation cover, and automatic weapons and four-wheel-drive vehicles have enabled unregulated hunting even in remote regions. The result has been a reduction in both the numbers and diversity of native plants and animals. Saudi Arabia's National Commission for Wildlife Conservation and Development (NCWCD) was created in 1986 to restore biodiversity through the management of a network of protected areas (Child & Grainger 1990). Where wildlife has been so reduced that natural recovery is not possible, the NCWCD has embarked on programs of restoration through release of captive-bred stock. The ostrich was identified as one of the components of the arid rangelands that required active restoration.

The NCWCD concentrated efforts around high-profile "flagship" species. These species are highly visible, charismatic, and traditionally valued; they include the Arabian oryx, the Houbara Bustard, and the ostrich. The loss of ostriches from the Arabian Peninsula was relatively recent; it is not uncommon to encounter people who remember when ostriches roamed the plains of Saudi Arabia. There is a real sense of sadness in Saudi Arabia that wildlife may be lost to future generations. Restoration of ostrich populations can therefore proceed with public support and can be used to raise public awareness of general conservation issues.

Selection of the Appropriate Subspecies

A decision was made by NCWCD to release the subspecies *Struthio camelus camelus* into Saudi Arabia to occupy the niche vacated by *Struthio camelus syriacus*. The following information was used to conclude that *S. c. camelus* is the most appropriate substitute. There are four subspecies of ostrich surviving in Africa. Two red-necked forms (*S. c. camelus* and *S. c. massaicus*); and two blue-necked forms (*S.(c.) molybdophanes* and *S. c. australis*). *S. c. camelus* was once distributed throughout North Africa, although regional extinction has reduced the range of this subspecies to a band that extends from Western Sahara through Mauritania, Mali, Niger, Chad,

Sudan, and Ethiopia, and possibly south to Uganda and Kenya (Freitag & Robinson 1993) (Fig. 1). *S. c. massaicus* is confined to Uganda, Kenya, and Tanzania. *S.(c.) molybdophanes* is restricted to the Horn of Africa, including Somalia, Ethiopia, and Kenya. *S. c. australis* is geographically most isolated, existing in Namibia, Botswana, Zimbabwe, and South Africa.

There has been considerable discussion about whether the Arabian Ostrich was red- or blue-necked. The written evidence is unequivocal: *S. c. syriacus* was red-necked. Early records from Arab authors describe the Arabian Ostrich as rather small and red-necked. The lexicographer Ibn Mandhur described the Arabian Ostrich in about 1311 in the monumental dictionary *Lisan Al-Arab*: "When the male ostrich (Dhaleem) comes into heat the color of his neck, chest and thighs becomes very red, but only the skin, not the feathers. This does not occur in the female." The name given in Arabic poetry to the male Arabian Ostrich in spring was *Al Khaadib*, meaning red at legs and neck. The Arabic verb *khadab* relates to the color red, used, for example, in reference to coloring the hands and feet with henna. The red color of the Arabian Ostrich attracted the attention of the great naturalist Al-Qazwini, who wrote of it in 1283 in the book *Agaib Al-Makbluqat* (Wonder of Creatures), comparing the reddening of the males to the ripening of the dates: "When summer arrives and the dates start to become red, the ostrich becomes red also; the intensity of redness in both dates and ostriches increases until such time as the reddening of the dates has finished."

The Arabian Ostrich was first described to Western science by Lord Rothschild at a meeting of the British

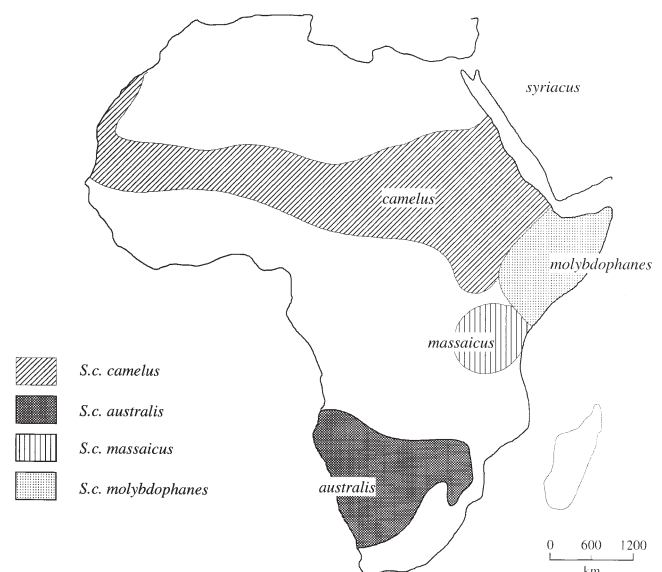


Figure 1. Approximate distribution of the four extant African subspecies of ostrich in relation to the Arabian Peninsula and the extinct Arabian form (*S. c. syriacus*).

Ornithologists' Club in 1919. He described it from the skins of two fully grown birds obtained from the Syrian desert as ". . . having neck and legs light red . . ." and assigned the subspecific name *syriacus* to distinguish it from the North African red-necked form (Rothschild 1919).

The most parsimonious explanation for the origin of *S. c. syriacus* is as an extension of the range of the nominate form, *S. c. camelus*, into Arabia, possibly via a land bridge between Sinai and the Egypto-Somalian domain. The ostriches in Arabia would have become more isolated geographically by the firm establishment of the Red Sea and Gulf of Suez in the late Pliocene, before about 2 million years ago. Some biotic interchanges may still have been possible across the Sahara-Arab desert belt along the Egyptian-Sinai-Israel passageway (Tchernov 1989).

The proximity of Africa and the Arabian Peninsula at the southern extreme of the Red Sea, between Djibouti and Yemen, allows for the possibility of a link between the blue-necked *S.(c.) molybdophanes* and a southern subpopulation of the Arabian Ostrich recorded along the fringes of the Rub' Al Khali until 1910 (Jennings 1986). There is evidence of land connections between Africa and southern Arabia around 53,000, 34,000, and 25,000–11,000 years before the present (Delany 1989). Such an interchange by ostriches, however, is unlikely because it would presuppose movement by *S.(c.) molybdophanes* across the Asir Mountain Range in southern Saudi Arabia or across the extension of the Asir, Hadhramaut, and Mahra Plateaux and the Kaur Mountains in Yemen, the highest mountain ranges in Arabia.

Both extinct and extant forms of ostrich are accorded only subspecific status. The existing subspecific forms appear to be largely geographically isolated: *S. c. australis* from the other forms by the "miombo" woodlands of Tanzania, Zambia, northern Angola, and Zaire and *S.(c.) molybdophanes* by the Great Rift Valley (Freitag & Robinson 1993). *S. c. syriacus* was interbred with *S. c. australis* on South African ostrich farms to improve stock for the feather trade (MacLean 1985). This apparently free interbreeding cannot be taken as proof of closer relatedness between *syriacus* and *australis* than between *syriacus* and other forms because *S. c. camelus* too was interbred with *S. c. australis* (de Mosenthal & Harting 1877; Freitag & Robinson 1993). *S. c. camelus* is also capable of interbreeding with *S.(c.) molybdophanes* (H. Mendelssohn, personal communication). It is probable that all extant forms could interbreed if geographical barriers were removed.

Freitag and Robinson (1993) examined the phylogenetic patterns of mitochondrial DNA of the four extant subspecies. They found large phylogenetic separation between *S. c. camelus* and all other forms and between *S.(c.) molybdophanes* and *S. c. massaicus* and *molybdophanes* and *australis*. A red-necked Arabian form, with *S. c. camelus* origins, would share and perhaps ex-

tend the degree of phylogenetic separation from the other forms. An albeit improbable extension by the blue-necked *S.(c.) molybdophanes* into southern Arabia is intuitively unlikely to have given rise to a separate subspecies of red-necked birds. There is no reason to believe the isolated *S. c. massaicus* could have given rise to an Arabian form, and the blue-necked *S. c. australis*—for both phenotypic and geographic reasons—is the least likely candidate for closest living relative to *syriacus*. Genetic comparisons between *S. c. syriacus* and *S. c. camelus* are currently being made (T. Robinson, personal communication).

Available evidence indicates that the Arabian Ostrich was red-necked. The most likely evolutionary origin of the Arabian *S. c. syriacus* subspecies was from an eastward extension and eventual isolation by the Red Sea of the nominate subspecies, the red-necked *S. c. camelus*. This would make *S. c. camelus* the closest living relative of the extinct Arabian Ostrich and therefore the most appropriate subspecies for any reintroduction program in Arabia.

S. c. camelus is almost extinct in Western Sahara, and hunting and egg collection has caused local extinction over large areas of North Africa, making survival of the subspecies unlikely without protection (Cramp & Simmons 1977). The establishment of new populations of *S. c. camelus* in large protected areas in Arabia would contribute to the preservation of the form.

Feasibility

Availability of suitable habitat within the former range of the Arabian Ostrich will be fundamental to the success of any release programs. The Arabian Ostrich's former range included large areas in northern and southern Saudi Arabia (Jennings 1986), and it is likely that much of the central region was also occupied by ostriches. Protection from hunting, and provision of areas in which vegetation recovery has been possible through regulation of livestock, are necessary for the restoration of ostrich populations in northern Saudi Arabia. Within the northern range the NCWCD administers over 15,000 km² of protected area, within which hunting is prohibited and grazing by domestic livestock is controlled. The areas have been protected for 10 years and currently support healthy populations of ibex (*Capra ibex*) and sand gazelle (*Gazella subgutturosa*).

In the south lies the 'Uruq Bani Ma' Arid Protected Area, a 5000-km² reserve straddling a portion of the western edge of the great sand desert, the Rub' Al Khali, where it is possible to find fragments of ostrich eggshell buried in the sand. Whereas hunting was probably the main cause of the disappearance of the northern population of *S. c. syriacus* in the 1930s, the Rub' Al Khali population had evidently been in decline for a century before its disappearance, probably by 1910 (Jennings 1986). The loss of

the southern ostrich population before the availability of modern firearms hints that this may have been due to factors other than hunting. Increasing aridity may have contributed to the southern extinction and may continue to limit prospects for ostrich restoration in the south of Saudi Arabia. The fenced Mahazat as-Sayd Protected Area encompasses over 2200 km² of *Acacia* steppe habitat in central Saudi Arabia and may provide suitable habitat for ostriches. The name of the nearby town of Dhaleem (male ostrich) and oral tradition give evidence of the former presence of ostriches locally.

A Jordanian conservation program maintains a small captive population of both *S. c. camelus* and the blue-necked *S.(c.) molybdophanes* (K. Irani, personal communication). Release of animals from the founder blue-necked population into areas just north of the Saudi Arabia-Jordan border could result in mixing with any red-necked form released into Saudi Arabia's northern protected areas. International coordination of release programs for Arabian oryx are being extended to cover conservation projects with possible cross-border consequences, though currently no ostrich releases are being planned by Jordanian conservation authorities (K. Irani, personal communication). *S. c. camelus* has been captive bred in Israel for over 20 years and has been proposed as a candidate for future substitution (Mendelssohn 1992).

During the last 5 years there has been an increased interest in commercial ostrich farming in Saudi Arabia. Farm stock has come primarily from the United States and probably has origins in South Africa, where a hybrid black-necked form is commercially farmed. The black-necked ostrich is the result of generations of interbreeding of the various subspecies; selection has been driven by feather quality and protein production. In Saudi Arabia a proliferation of ostrich farms using black-necked forms introduces a risk of accidental releases and interbreeding with free-ranging red-necked ostriches. A similar problem is posed by accidental releases of hybrid ostriches from private animal collections.

Founders for the Saudi Arabian ostrich captive-breeding and restoration program come from wild-born chicks in the Sudan and from private collections in the Middle East. Work is underway to develop ostrich reintroduction techniques through trial releases into the Mahazat as-Sayd Protected Area, where some breeding by free-ranging ostriches has taken place (Seddon 1997).

Conclusion

The release of animals into suitable habitat is a seductive option for the restoration of depleted or locally extinct wildlife populations, but to have any chance of success such projects cannot be undertaken lightly. Even when a subspecies has become extinct, opportunities may exist for the release of a related form into vacated habitat. The

selection of a substitute requires careful consideration of the suitability and availability of subspecific forms. Assessment of subspecies suitability should include genetic and ecological compatibility, but, as in the case of the Arabian Ostrich, lack of information about the extinct form may result in decisions based primarily on phenotypic or geographical similarities. Without support from genetic analyses of museum tissue samples and detailed life-history information, the *S. c. camelus* subspecies was chosen as a substitute on the basis of phenotype, distribution, and conservation value. It remains to be seen if *S. c. camelus*, from the semiarid woodlands of Sudan, will produce offspring that can survive the arid steppe deserts of Saudi Arabia.

Acknowledgments

Wildlife conservation in Saudi Arabia is carried out with the support of His Royal Highness Prince Saud Al Faisal and of A. H. Abuzinada. Y. van Heezik, M. Stanley Price, K. Dunham, G. Meffe, E. Main, and two anonymous referees provided constructive criticism of the manuscript. F. Vire and P. Paillat compiled historical references. A. Boug and M. Shobrak translated Arabic source material.

Literature Cited

- Avise, J. C. 1995. Mitochondrial DNA polymorphism and a connection between genetics and demography of relevance to conservation. *Conservation Biology* 9:686-690.
- Balmford, A., G. M. Mace, and N. Leader-Williams. 1996. Designing the ark: setting priorities for captive breeding. *Conservation Biology* 10:719-727.
- Brocke, R. H., and K. A. Gustafson. 1992. Lynx *Felis lynx* in New York State. Re-introduction News 4:6-7.
- Child, G., and J. Grainger. 1990. A system plan for protected areas for wildlife conservation and sustainable rural development in Saudi Arabia. National Commission for Wildlife Conservation and Development (NCWCD), Riyadh, and World Conservation Union, Gland, Switzerland.
- Clark, J. D. 1996. Black bear repatriation to Cumberland Plateau. Re-introduction News 12:12-13.
- Clark, T. W. 1994. Restoration of the endangered black-footed ferret: a 20-year overview. Pages 272-297 in M. L. Bowles and C. J. Whelan, editors. Restoration of endangered species. Cambridge University Press, Cambridge, United Kingdom.
- Cramp, S., and K. E. L. Simmons. 1977. The birds of the Western Palearctic. Volume 1. Ostriches to ducks. Oxford University Press, Oxford, United Kingdom.
- Delany, M. J. 1989. The zoogeography of the mammal fauna of southern Arabia. *Mammal Review* 19:133-152.
- de Mosenthal, J., and J. E. Harting. 1877. Ostriches and ostrich farming. Trubner & Co., London.
- Freitag, S., and T. J. Robinson. 1993. Phylogenetic patterns in mitochondrial DNA of the ostrich (*Struthio camelus*). *Auk* 110:614-622.
- Gilpin, M. E. 1987. Spatial structure and population vulnerability. Pages 125-140 in M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.
- Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19-34 in M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

- Goodman, D. 1987. The demography of chance extinction. Pages 11–34 in M. E. Soulé, editor. *Viable populations for conservation*. Cambridge University Press, Cambridge, United Kingdom.
- Green, R. E. 1997. The influence of numbers released on the outcome of attempts to introduce exotic birds species to New Zealand. *Journal of Animal Ecology* **66**(1):25–35.
- Hughes, I. 1994. British zoos and the little brown moths. *Re-introduction News* **9**:11–12.
- IUCN. 1995. Guidelines for Re-introductions. Annex 6 to the minutes of the 41st meeting of council. Gland, Switzerland.
- IUCN. 1998. Guidelines for Re-introductions. Prepared by the IUCN/SSC Re-introduction Specialist Group. Gland, Switzerland and Cambridge, United Kingdom.
- Jennings, M. C. 1986. The distribution of the extinct Arabian ostrich, *Struthio camelus syriacus*, Rothschild, 1919. *Fauna of Saudi Arabia* **8**:447–461.
- Kleiman, D. G., B. B. Beck, J. M. Dietz, and L. A. Dietz. 1988. Costs of a reintroduction and criteria for success: accounting and accountability in the golden lion tamarin conservation program. Pages 125–144 in J. H. W. Gipps, editor. *Beyond captive-breeding: re-introducing endangered mammals to the wild*. Symposium of the Zoological Society of London 62. Clarendon Press, Oxford, United Kingdom.
- Lieberman, A., J. V. Rodriguez, J. M. Paez, and J. Wiley. 1993. The re-introduction of the Andean condor into Columbia, South America. *Oryx* **27**(2):83–90.
- Macdonald, D. W., F. H. Tattersall, E. D. Brown, and D. Balharry. 1995. Reintroducing the European beaver to Britain: nostalgic meddling or restoring biodiversity. *Mammal Review* **25**:161–200.
- MacLean, G. L. 1985. Roberts' birds of southern Africa. John Voelcker Bird Book Fund, Cape Town.
- Mendelssohn, H. 1992. Return of biblical fauna. *Re-introduction News* **4**:10–11.
- Moore, D. E., III, and R. Smith. 1988. The red wolf as a model for carnivore re-introductions. Pages 263–278 in J. H. W. Gipps, editor. *Beyond captive-breeding: re-introducing endangered mammals to the wild*. Symposium of the Zoological Society of London 62. Clarendon Press, Oxford, United Kingdom.
- Nelson, G. 1989. Species and taxa: systematics and evolution. Pages 60–81 in D. Otte and J. A. Endler, editors. *Speciation and its consequences*. Sinauer Associates, Sunderland, Massachusetts.
- Possiel, W., R. E. Saunier, and R. A. Meganck. 1995. In-situ conservation of biodiversity. Pages 7–20 in R. E. Saunier and R. A. Meganck, editors. *Conservation of biodiversity and the new regional planning*. Organization of American States and World Conservation Union, Gland, Switzerland.
- Pullin, A. 1993. Large copper butterfly in England. *Re-introduction News* **6**:10–11.
- Rand, D. M. 1996. Neutrality tests of molecular markers, and the connection between DNA polymorphism, demography, and conservation biology. *Conservation Biology* **10**:665–671.
- Risser, P. G. 1995. Biodiversity and ecosystem function. *Conservation Biology* **9**:742–746.
- Rothschild, L. 1919. *Bulletin of the British Ornithologists' Club* **39**:81–83.
- Ryder, O. A. 1988. Przewalski's horse: putting the wild horse back in the wild. *Oryx* **22**(3):154–157.
- Seddon, P. J. 1997. Ostrich update, Saudi Arabia: wild ostriches breed in the Arabian Peninsula for the first time in over 40 years. *Re-introduction News* **14**:16–17.
- Seddon, P. J., M. Saint Jalme, Y. van Heezik, P. Paillat, P. Gaucher, and O. Combreau. 1995. Restoration of houbara bustard populations in Saudi Arabia: developments and future directions. *Oryx* **29**(2):136–142.
- Snyder, N. F. R., S. R. Derrickson, S. R. Beissinger, J. W. Wiley, T. B. Smith, W. D. Toone, and B. Miller. 1996. Limitations of captive breeding in endangered species recovery. *Conservation Biology* **10**:338–348.
- Stanley Price, M. R. 1989. *Animal re-introductions: the Arabian oryx in Oman*. Cambridge University Press, Cambridge, United Kingdom.
- Stanley Price, M. R., P. S. Soorae, and A. F. Falcon. 1998. General aims and principles of re-introductions. Pages 11–20 in *The re-introduction of the lynx into the Alps: proceedings of the 1st SCALP conference*. Environmental Encounters 38. Council of Europe Publishing, Engelberg, Switzerland.
- Tchernov, E. 1989. The biogeographical history of the southern Levant. Pages 159–250 in Y. Yom-Tov and E. Tchernov, editors. *The zoogeography of Israel*. Monographiae biologicae. Volume 62. Dr. W. Junk, Dordrecht, The Netherlands.
- Templeton, A. R. 1989. The meaning of species and speciation: a genetic perspective. Pages 3–27 in D. Otte and J. A. Endler, editors. *Speciation and its consequences*. Sinauer Associates, Sunderland, Massachusetts.
- van Dierendonck, C., and M. F. Wallis de Vries. 1996. Ungulate re-introductions: experiences with the Takhi or Przewalski horse (*Equus ferus przewalskii*) in Mongolia. *Conservation Biology* **10**:728–740.
- Walker, B. 1995. Conserving biological diversity through ecosystem resilience. *Conservation Biology* **9**:747–752.
- Wallace, M. 1992. California condor status report. *Re-introduction News* **5**:4–5.
- Walter, H. S. 1993. Socorro dove in Mexico. *Re-introduction News* **7**:8.
- Wolf, M. C., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Conservation Biology* **10**:1142–1154.
- The World Zoo Organization (IUDZG)/The Captive Breeding Specialist Group (CBSG). 1993. Executive summary of the world zoo conservation strategy: the role of the zoos and aquaria of the world in global conservation. Chicago Zoological Society, Illinois.

